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SITE AND PREY SELECTION BY WINTERING BLACK-TAILED GODWIT *LIMOSA LIMOSA ISLANDICA* FEEDING ON SEAGRASS BEDS AND BARE MUDFLATS ON THE CENTRAL ATLANTIC COAST OF FRANCE

Frédéric ROBIN[1*], Francis MEUNIER[2], Frédéric CORRE[3], Emmanuel JOYEUX[4], Marie-Laure CAYATTE[5], Philippe DELAPORTE[6], Jean-Christophe LEMESLE[7], Philippe PINEAU[1] & Pierrick BOCHER[1]

[1] Laboratory Littoral Environnement et Sociétés, UMR 7266 LIENSs CNRS- University of La Rochelle, 2 Rue Olympe de Gouges. F-17042 La Rochelle.
[2] Conservatoire d'espaces naturels de Picardie, 1, Place Ginkgo - Village Oasis. F-80044 Amiens Cedex 1.
[3] Réserves Naturelles de la Baie de l'Aiguillon, Ligue pour la Protection des Oiseaux-LPO, Ferme de la Prée Mizotière. F-85450 Sainte Radegonde des Noyers.
[4] Réserves Naturelles de la Baie de l'Aiguillon, Office National de la Chasse et de la Faune Sauvage ONCFS, Ferme de la Prée Mizotière. F- 85450 Sainte Radegonde des Noyers.
[5] Réserve Naturelle des Marais d'Yves, LPO, Ferme de la Belle Espérance. F-17340 Yves.
[6] Réserve Naturelle de Moëze-Oléron, LPO, Plaisance. F-17180 Saint-Froult.
[7] Réserve Naturelle de Lilleau des Niges, LPO, Route du Vieux Port, F-17880 Les Portes en Ré.
*Author for correspondence: Tel+33 5 45 46 83 94. Fax: + 33 5 45 46 82 64. Email: frobin02@gmail.com

RÉSUMÉ.— *Sélection des sites et des proies par les Barges à queue noire* Limosa limosa islandica *s'alimentant sur les herbiers de zoostères et les vasières du centre de la côte atlantique française*.— Dans une population en expansion, certains individus sont voués à explorer et exploiter de nouveaux habitats de moindre qualité. Sur la façade ouest européenne, la Barge à queue noire *Limosa limosa islandica*, qui se reproduit exclusivement en Islande, est l'une des rares espèces de limicoles avec une tendance démographique positive. Les côtes françaises accueillent 28 % de la population au milieu de l'hiver, le reste se distribuant sur les îles britanniques et la péninsule ibérique. Contrairement à la Grande Bretagne et l'Irlande, la population française se concentre sur un nombre restreint de sites mais avec de fortes concentrations. Les Pertuis Charentais accueillent plus de 65 % de la population nationale (*ca* 18 000 individus). Dans cette étude, nous décrivons comment la sélection des proies et les stratégies d'alimentation en milieux intertidaux sont liées à la sélection des sites à l'échelle locale and peuvent expliquer la distribution des oiseaux en période de non reproduction. La sélection des sites et des espèces-proies par les barges a été étudiée par la description du régime alimentaire et de la ressource trophique sur six zones d'alimentation sur les quatre principaux sites hivernages. Dans les Pertuis Charentais, il a été confirmé que ces barges occupent une niche écologique herbivore sur le nouveau site d'hivernage de l'île de Ré, où elles s'alimentent de Zostères naines *Zostera noltii*. La barge garde un régime carnivore sur les sites continentaux, où elle s'alimente principalement du bivalve *Macoma balthica*. Sur ces sites, les barges ciblent la proie la plus rentable. À l'exception du dérangement humain, la distribution des individus dans les Pertuis Charentais semble être déterminée par la distribution, l'abondance et l'accessibilité de seulement deux espèces-proies parmi un large éventail d'espèces benthiques.

SUMMARY.— In expanding populations, individuals may gradually be constrained to use new sites with non-optimal quality habitats. On the coast of Western Europe, the Black-tailed Godwit *Limosa limosa islandica*, breeding in Iceland, is one of the rare shorebird species with an increasing population trend. The coast of France hosts 28 % of this population in mid-winter, with the remainder of the population wintering in the British Isles or in the Iberian Peninsula. Unlike godwits in Britain and Ireland, they are distributed among a small number of sites across France and are concentrated in high numbers at each. The Pertuis Charentais hosts up to 65 % of the Black-tailed Godwits recorded nationally (*ca* 18 000 individuals). In this study, we describe how prey selection and feeding strategies in intertidal areas are linked to site selection at the local scale and could explain the distribution of birds during the non-breeding period. The selection of site and prey species by godwits was studied by describing the diet and food supply of the species in six feeding areas at four local wintering sites. In the Pertuis, it has been confirmed that they have expanded into a herbivorous niche at newly established wintering sites on Ré Island where they feed on the seagrass *Zostera noltii.* The species remains strictly carnivorous at continental sites, where it forages actively on the bivalve *Macoma balthica*. Within sites, godwits target the most profitable preys. With the exception of human disturbances, the distribution of individuals within the Pertuis seems to be determined by the distribution, abundance and accessibility of only two prey species among a large array of macrofaunal species.

How animals distribute themselves within their feeding and breeding grounds according to temporal and spatial scales is an important issue in terms of species and habitat conservation (Jonzén, 2008). When explaining distribution, it is usually assumed that individuals have the perfect knowledge of the quality of their habitats such that their distribution reflects multiple hierarchical processes of optimal habitat selection (Piersma & van Gils, 2011). When selecting their feeding habitat, free-living animals are thought to adopt strategies of food selection that minimize the time and energy spent for a given quantity of food ingested (Stephens & Krebs, 1986). For instance, the distribution of overwintering shorebirds and their numbers at a regional scale can be predicted by the distribution and availability of their benthic prey species in the intertidal mudflats (Colwell & Landrum, 1993; Goss-Custard, 1968; Kalejta & Hockey, 1991; Nehls & Tiedemann, 1993; Piersma, 1993; Wilson, 1990).

On the coast of Western Europe, the Pertuis Charentais in France is a complex of estuarine bays and islands located on the East Atlantic Flyway and is recognized as being a site of international importance for many migrant and wintering waterbirds (Delany *et al.*, 2009). During the non-breeding period, the Pertuis hosts 65 % of the Icelandic population of the Black-tailed Godwit *Limosa limosa islandica* in France (ca. 18 000 individuals in January 2010). Unlike godwits in Britain and Ireland, godwits are here concentrated in a small number of sites across France (Caillot, 2006). In the Pertuis, the wintering population is distributed among four sites that are totally or partly enclosed in nature reserves. During the winter period, the godwits at these sites forage and feed exclusively on two different habitats including seagrass beds and bare mudflats (Robin *et al.*, 2013).

The aim of the study was to complete the composition of godwits' diet previously described in Robin *et al.* (2013) and to describe diet in a new site never studied before. The trophic resources are spatially described on large sectors of feeding area compared to the previous studies. After description of diet and trophic resource of birds the question raised is what is the spatial match between godwits and their preys? Prey selection was studied with respect to the availability and the digestive quality of the main preys. We hypothesize that individuals are not distributed according to the total available mudflat surface per site but according to the densities and availability of the highest quality prey at each site.

METHODS

STUDY SITES

The coast of the Pertuis Charentais is characterised by a succession of soft intertidal mudflats in bays or estuaries (Fig. 1). The four study sites for the species were (1) the traditional wintering site of Aiguillon Bay, and the more recently used sites of (2) Ré Island, (3) Yves Bay and the Charente Estuary and (4) Marennes-Oléron Bay (Robin *et al.*, 2013).

Aiguillon Bay (AI, 46°17'N, 01°10'W) comprises a large tidal area with a bare muddy surface (Tab I). We focused our sampling effort on the Eastern part of the bay (Charente-Maritime side, AI_C, 2,306 ha) including the main feeding area, and the Western part (Vendée side, AI_V, 1,400 ha), which is used secondarily by the species. The entire bay is contained within two nature reserves.

Ré Island (RI) is located in the north of the Pertuis Charentais, just 10 km away from AI. On the northern side, two intertidal mudflats are enclosed by small bays called the "Fier d'Ars" (RI_{FA}, 46°13'N, 1°29'W, 570 ha,) and "Fosse de Loix" (RI_{FL}, 46°12'N, 1°25'W, 230 ha,). The Fier d'Ars has heterogeneous sediment characteristics. The southern part of the bay is rather muddy and is covered by seagrass beds (*Zostera noltii*). The northern part of the bay is characterized by sandbanks. Only the western part of the bay and the high tide roost in the saltpans are contained within the nature reserve of "Lilleau des Niges". The Fosse de Loix is a small bay east of RI_{FL} and is also covered with seagrass beds.

The *Charente Estuary* (CE, 45°57'N, 1°5'W) is located between the Yves and Marennes-Oléron bays. The Charente is the largest estuary in the Pertuis Charentais. At its mouth, the river is bordered by large intertidal mudflats, spreading across 350 ha to the north and 710 ha to the south.

Marennes-Oléron Bay (MO, 45°55'N, 01°10'W) is a large bay of 17,500 ha in the southern part of the Pertuis Charentais. The two sectors selected were the Eastern part of Oléron Island (MO_O, 2,380 ha) and the mudflats at Moëze along the continental coast (MO_M, 3,360 ha). Intertidal habitats are heterogeneous in the Oléron sector with a patchwork of

muddy and sandy areas covered by seagrass beds (Lebreton *et al*., 2009). The MO_M sector has a bare muddy substrate with alternating runnels and ridges.

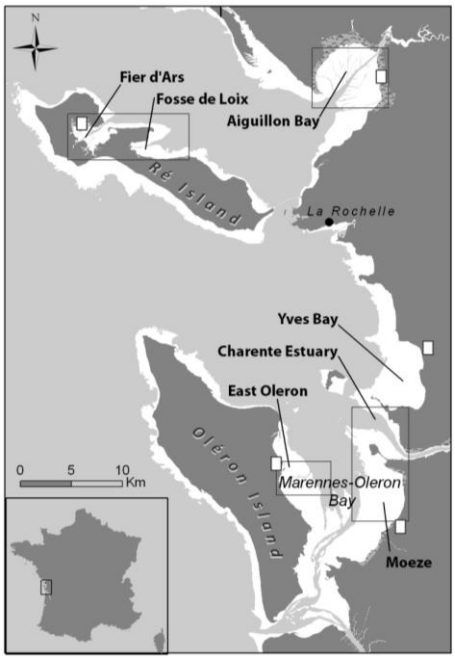

Figure 1.— Location of the four study sites and six study feeding areas in the Pertuis Charentais. Sampling sectors are bordered by a dark line; white rectangles indicating the location of the main high tide roost at each site.

TABLE I

Number of stations sampled for macrofauna, and number of droppings collected per site. Sediment characteristics are expressed as mean grain size of sediment and percentage of silt (sediment < 63 µm)

Study sites and sectors	Sampling dates	N samples		Sediment characteristics		Surface covered	
		Stations (% by foot)	Droppings (pool of 25)	Median grain	% of mud < 63 µm	Grid (ha)	% of whole feeding area
Aiguillon Bay							
Vendée (AIv)	12 &13 Jan	64 (22%)	-	21 ± 6	75%	244	17%
Charente (AIc)	12 to 15 Jan	109 (36%)	7	20 ± 13	78%	392	17%
Ré Island							
Fier d'Ars (RI_{FA})	1 to 5 Sep	98 (100%)	2	57 ± 69	59%	392	69%
Fosse de Loix (RI_{FL})	12 Feb	82 (4%)	1	11 ± 2	81%	244	100%
Charente Estuary (CE)	15 & 22 Sep	87 (34%)	2	17 ± 10	82%	550	52%
Marennes-Oléron Bay							
Moëze (MO_M)	26 & 27 Jan	58 (6%)	2	20 ± 14	78%	400	12%
Oléron (MO_O)	9 & 12 Feb	67 (100%)	-	76 ± 28	39%	400	17%

GODWIT COUNTS

Black-tailed Godwits on the mudflats were counted each month from July 2008 to June 2009 during the ebb tide or on the high tide roosts by the managers and technicians of the nature reserves. Birds were counted simultaneously at each site by observers using telescopes.

FOOD RESOURCE SAMPLING AND TREATMENT

The distribution, densities and biomasses of macrofaunal species and seagrass were determined by extracting sediment cores at predetermined stations (Bocher *et al*., 2007). The sampling grids were predetermined according to the size of each site, in order to cover the majority of the intertidal mudflats. Gridlines were fixed at intervals of 250 m at all

sites except on Ré Island (200 m intervals). The sampling stations (shown as crosses on Figs 5 & 6) were located by GPS (WGS84 as the map datum). From September 2008 to February 2009, a total of 575 sampling stations were visited either on foot or by boat (Tab. I).

The dates of sampling per site were chosen according to the peak frequentation by godwits recorded in previous years (Bocher *et al*., 2013a). The macrofauna was sampled systematically according to the method described in Bocher *et al*. (2007). In brief, for stations visited on foot, one sediment core covering 0.018 (1/56) m² was extracted to a depth of 20–25 cm. For those visited by boat, two sediment cores each covering 0.008 m² (20–25 cm depth) were extracted, giving a total surface area of 0.016 m². A previous study found that sampling on foot and by boat yielded identical density estimates (Kraan *et al.*, 2009). After sieving, all living molluscs and crustaceans were placed in a plastic bag and stored at -20 °C for subsequent analysis in the laboratory. Annelids were conserved in 70 % ethanol. At every 1 km intersection of the grids, a sediment sample with a 5 cm diameter core was extracted to a depth of 4–5 cm to determine sediment characteristics (Tab. I). The median particle size and the percentage of silt (fraction < 63 µm) of sediments were determined using a Coulter LS 230 particle size analyser.

In the laboratory, all organisms were identified to species level whenever possible and then counted. Individuals were measured to a precision of 0.1 mm. For molluscs, the dry mass (DM) of the shell and meat was weighed individually after 3 days at 55 °C, and the ash free dry mass (AFDM) was deducted after incineration at 550 °C for 5 hours. The biomasses of worms and crustaceans were not calculated because these species were not found in the birds' diet.

FROM TOTAL TO HARVESTABLE BIOMASS

In a previous study we showed that less than 1 % of *Macoma balthica* and 10 % of *Scrobicularia plana* (Robin *et al.*, 2013) were located below the maximum depth reachable by the culmen of the birds (a maximum of 105 mm for females, Bocher *et al*., 2013b). Consequently in this study, all the bivalves in samples were considered as accessible for godwits. From the total biomass, we determine the precise harvestable fraction of the molluscs' biomass per station considering the lengths of prey reconstructed from remains found in the droppings: (1) excessively large prey (> 16 mm) found in the sediment that could not be ingested and (2) excessively small unprofitable prey (< 4 mm) were excluded (Quaintenne *et al*., 2011). The seagrass biomass was described as DM ($g.m^{-2}$) after drying (at 55 °C) with leaves and rhizomes being considered together.

RECONSTRUCTION OF GODWIT DIET

The godwit's diet was reconstructed from droppings collected within each feeding area sampled (Tab. I). Each dropping sample consisted of one set of 25 individual droppings, pooled. In the laboratory, the diet was reconstructed by combining the protocols for hard-shelled prey (Dekinga & Piersma, 1993) and for soft worm determination (Scheiffarth, 2001). In order to compare the herbivorous and carnivorous diets, all dietary compositions per site were expressed as energy content (kilojoules, kJ). Vegetable matter contains insoluble fibres that are considered to be indigestible for most bird species (Klasing, 1998). Here, the vegetable fibres found in the droppings were considered to comprise the indigestible fraction of the seagrass *Z. noltii*, which has been estimated to comprise 46.3 ± 7.4 % of the ingested DM calculated for Brent Geese, *Branta bernicla* (unpublished data, Dalloyau, 2008). The digestible part (the part not remaining in the droppings) was expressed using a mean energy content of 16.893 $kJ.g^{-1}_{DM}$ (For *Zostera noltii* in Oléron Island, unpublished data, Dalloyau, 2008), and for molluscs, the energy content was expressed using the equivalent of 22 $kJ.g^{-1}$ for AFDM established by Zwarts & Wanink (1993).

PREY QUALITY

For molluscivorous shorebirds, the rate of food intake is limited by the rate of digestion (Quaintenne *et al*., 2010; van Gils *et al*., 2005), and thereby prey items were ranked on the basis of their digestive quality rather than by their profitability. Digestive quality was expressed as the index $daAFDM_{flesh}/DM_{shell}$, where *d* is the energetic density of the flesh (22 $kJ.g^{-1}$ $AFDM_{flesh}$; in Zwarts & Wanink, 1993) and *a* is the assimilation efficiency coefficient, which was equal to 0.8 and was assumed to be constant across individual birds and prey items (assumed for Red Knot *Calidris canutus* in Piersma *et al.*, 1994).

RESULTS

SEASONAL OCCURRENCE OF GODWITS

In the depths of winter 2008–2009, the mean number of godwits in the Pertuis was 11 295 ± 1187 individuals (mean ± SD for the period October to January). The local population reached a maximum of ca 14 000 individuals in February, as a consequence of a sudden increase from 2800 to 8000 individuals in MO. Godwits were not equally distributed and their phenology differed

between the four sites (Fig. 2). From October to January, AI welcomed 48.0 ± 7.1 % (mean ± SD) of the Pertuis population, while 23.1 ± 4.2 % of the population was present on RI, 12.1 ± 10.5 % in YB and 16.9 ± 13.8 % in MO. In Figure 2b, the variation in godwit numbers per site is expressed in relation to the surface area of available mudflats considered (number of individuals per hectare). The overall density of godwits was stable between October and March with 1.4 ± 0.2 individuals per hectare in the Pertuis. At YB and MO, densities reached a maximum of 0.8 ± 0.2 individuals per hectare (Fig. 2b). On RI, densities were twice as high as in AI and corresponded, in November, to a density of 4.1 individuals per hectare.

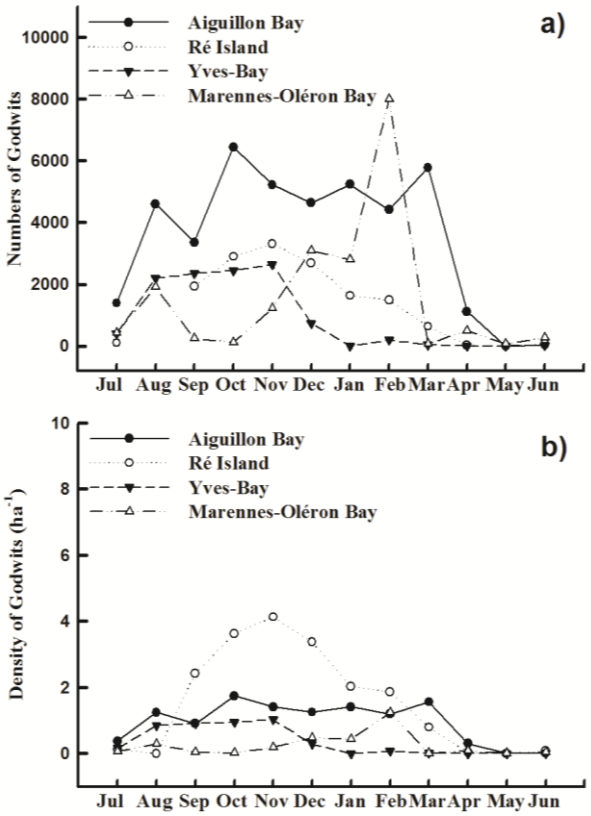

Figure 2.— Monthly variation in number (a) and density (b) of Black-tailed Godwits per site during the non-breeding period of the annual cycle 2008–2009 in the Pertuis Charentais.

TOTAL FOOD RESOURCE ABUNDANCE AND DENSITY

At all sites, *Hydrobia ulvae* was the most frequently occurring species (66 % in RI_{FL} to 98 % in MO_M), with the highest densities of all species (1028 ± 1265 individuals.m^{-2} in AI_C to 7733 ± 10 699 individuals.m^{-2} in $RI_{FA;}$ mean ± SD) and the highest biomass (1.0 ± 1.4 g_{AFDM}.m^{-2} in AI_V to 8.5 ± 12.0 g_{AFDM}.m^{-2} in RI_{FA}; Tab. II). Annelids were poorly represented except for the large worms *Nephtys hombergii* (46 and 50 % frequency of occurrence for AI_V and AI_C, respectively) and *Hediste diversicolor* (13 % and 17 % for AI_V and AI_C). The small worm *Notomastus latericeus* was common on RI, with a frequency of occurrence of 43 % and 54 % for RI_{LO} and RI_{FA}, respectively.

TABLE II

*Frequency of occurrence (Occ.), mean density (Dens.) and mean biomass (Biom. in AFDM) of macrofaunal species per feeding area at the study sites. The biomasses of polychaetes and arthropods were not available (these are indicated by *)*

Species	Aiguillon Bay						Ré Island						Charente Estuary			Bassin de Marrenes-Olèron					
	Charente-Maritime			*Vendée*			*Fier d'Ars*			*Fosse de Loix*						*Moëze*			*Oléron*		
	Occ. (%)	Dens. (ind.m^{-2})	Biom. (mg.m^{-2})	Occ. (%)	Dens. (ind.m^{-2})	Biom. (mg.m^{-2})	Occ. (%)	Dens. (ind.m^{-2})	Biom. (mg.m^{-2})	Occ. (%)	dens (ind.m^{-2})	Biom. (mg.m^{-2})	Occ. (%)	dens (ind.m^{-2})	Biom. (mg.m^{-2})	Occ. (%)	dens (ind.m^{-2})	Biom. (mg.m^{-2})	Occ. (%)	dens (ind.m^{-2})	Biom. (mg.m^{-2})
Polychaetes																					
Alitta succinea	<1	0	*	7	5	*	-	-	-	-	-	-	-	-	-	*	*	*	9	5	*
Notomastus latericeus	<1	1	*	-	-	-	43	195	*	54	93	*	1	3	*	*	*	*	22	57	*
Nephtys hombergii	46	48	*	50	42	*	9	9	*	1	1	*	-	-	-	*	*	*	6	3	*
Nephtys sp.	-	-		<1	1	*	-	-	-	-	-	-	-	-	-	*	*	*	7	4	*
Hediste diversicolor	13	15	*	17	14	*	2	2	*	-	-	-	-	-	-	*	*	*	7	5	*
Nereididae sp.	5	3	*	4	3	*	1	<1	*	3	6	*	-	-	-	*	*	*	10	6	*
Melinna palmata	-	-	-	-	-	-	1	<1	*	17	18	*	-	-	-	*	*	*	-	-	-
Cirratulidae sp.	-	-	-	-	-	-	14	21	*	-	-	-	-	-	-	*	*	*	-	-	-
Pygospio elegans	4	3	*	6	4	*	-	-	-	-	-	-	-	-	-	*	*	*	7	5	*
Owenia fusiformis	3	2	*	6	3	*	2	1	*	1	1	*	-	-	-	*	*	*	4	28	*
Arthropods																					
Gammarus sp.	-	-	-	-	-	-	2	1	*	17	29	*	-	-	-	-	-	-	-	-	-
Carcinus maenas	-	-	-	-	-	-	12	8	*	-	-	-	1	<1	*	-	-	-	-	-	-
Bivalves																					
Mytilus edulis	-	-	-	-	-	-	5	5	39	-	-	-	-	-	-	-	-	-	-	-	-
Nucula nitidosa	-	-	-	-	-	-	-	-	-	-	-	-	4	15	36	-	-	-	-	-	-
Cerastoderma edule	12	10	65	62	126	1876	58	158	6365	7	4	77	36	196	986	6	6		33	26	
Abra tenuis	14	20	16	25	22	18	51	181	107	8	6	8	4	2	3	33	49	17	16	23	17
Scrobicularia plana	35	251	3980	37	338	5629	21	24	389	33	32	784	40	186	2579	41	162	2932	31	36	811
Macoma balthica	73	120	365	60	68	246	5	3	19	3	2	15	64	178	664	45	98	470	7	4	9
Tellina tenuis	-	-	-	-	-		12	22	36	-	-	-	-	-	-	-	-	-	-	-	-
Mysia undata	<1	1	<1	-	-	-	-	-	-	7	12	*	-	-	-	-	-	-	-	-	-
Ruditapes spp.	6	5	111	7	7	313	47	87	3759	50	87	3237	20	18	41	8	7	224	25	21	1095
Gasteropods																					
Retusa obtusa	<1	0	<1	-	-	-	13	14	61	-	-	-	2	1	<1	9	7	3			
Cyclope neritea	<1	0	<1	-	-	-	17	22	1589	3	2	29	4	3	33	2	<1	66	6	5	187
Bittium reticulatum	-	-	-	-	-	-	6	8	99	-	-	-	-	-	-	-	-	-	-	-	-
Hydrobia ulvae	88	1028	995	92	2202	2381	70	7733	8583	66	1298	2264	83	2982	3639	98	1428	952	78	4586	4480
Littorina littorea	<1	1	21	-	-	-	35	78	638	21	24	200	-	-	-	-	-	-	4	3	16

Given the dietary composition of godwits, subsequent analysis of food resources is limited to the main prey species, comprising seagrass and bivalves. Seagrass occurred at only three sites (Fig. 3). The plant was found at 57 % of the stations in RI_{FA} with a mean DM of 115.5 ± 186.1$g_{DM}.m^{-2}$, at 79 % of the stations in RI_{FL} with a mean DM of 58.9 ± 52.9$g_{DM}.m^{-2}$ and at 73 % of the stations in MO_O with a mean DM of 45.7 ± 101.1$g_{DM}.m^{-2}$. Although their frequency of occurrence varied between sites, *S. plana* and *Cerastoderma edule* had the highest densities and biomasses of all bivalves (Table II). In seagrass habitats such as RI_{FA}, *C. edule* presented the highest biomass (6.4 ± 1.2$g_{AFDM}.m^{-2}$). On bare mudflat habitats, *S. plana* had the highest biomass, ranging from 2.6 ± 5.0$g_{AFDM}.m^{-2}$ in CE to 5.7 ± 8.9$g_{AFDM}.m^{-2}$ in AI_V. The clams *Ruditapes spp*. also showed high biomasses in seagrass habitats (Tab. II). The main prey species, *M. balthica*, had a lower biomass, ranging from 0.4 ± 0.5$g_{AFDM}.m^{-2}$ to 0.6 ± 1.0$g_{AFDM}.m^{-2}$, at AI_C and CE, respectively. Nevertheless, compared to other bivalves, *M. balthica* occurred at a higher number of sampling stations, being found on 45 to 73 % of the sampled surface area on bare mudflats (Tab. II).

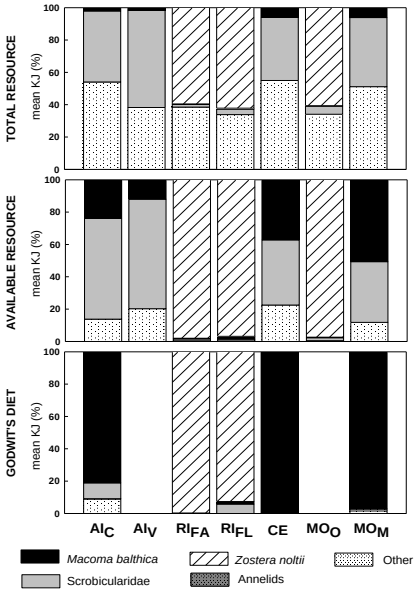

Figure 3.— Proportion of total (a), available (b) and consumed (c) biomass of mollusc species and seagrasses (mean percentage of kJ per m^2 for a-b and per dropping in c) for godwits in each sector: AI_C, Charente-Maritime part of Aiguillon Bay; AI_V, northern part of Aiguillon Bay; RI_{FA}, Fier d'Ars* on Ré Island; RI_{FL}, Fosse de Loix* on Ré Island; CE, Charente Estuary; MO_O, Oléron sector* of Marennes-Oléron Bay; MO_M, Moëze sector of Marennes-Oléron Bay (* indicates sites with seagrass beds). (a) The total biomasses in mudflats, (b) is biomasses of the potential prey ingested of (a) (species preyed in ingested sizes and not too deep), (c) is biomass reconstructed from faeces analysis.

GODWIT DIET

Diets were established from a total of 350 droppings collected inside the benthos sampling grid of the main feeding areas (Tab. I). No droppings could be collected in AI_V or were found in MO_O. On bare mudflats of AI_C, CE, and MO_M, godwits fed exclusively on three bivalve species: *Macoma balthica*, *Abra tenuis* and *Scrobicularia plana* (Fig. 3). Only a few remains of large worms (Nereididae) were found in droppings from MO_M and AI_C, along with some fragments of the gastropod *Hydrobia ulvae* (7.8 % of the diet for MO_M). The bivalve *M. balthica* contributed

most to consumed energy on bare mudflats (81.1 % in AI_C, 99.9 % in CE and 97.2 % in MO_M; Fig. 3). On RI, droppings were composed mainly of seagrass remains, corresponding to 99.7 % and 92.5 % of the energy content in RI_{FA} and RI_{FL}, respectively (Fig. 3). The rest of the diet was composed of Scrobiculariidae (small *S. plana* and/or large *A. tenuis*), representing up to 5.8% of the energy content.

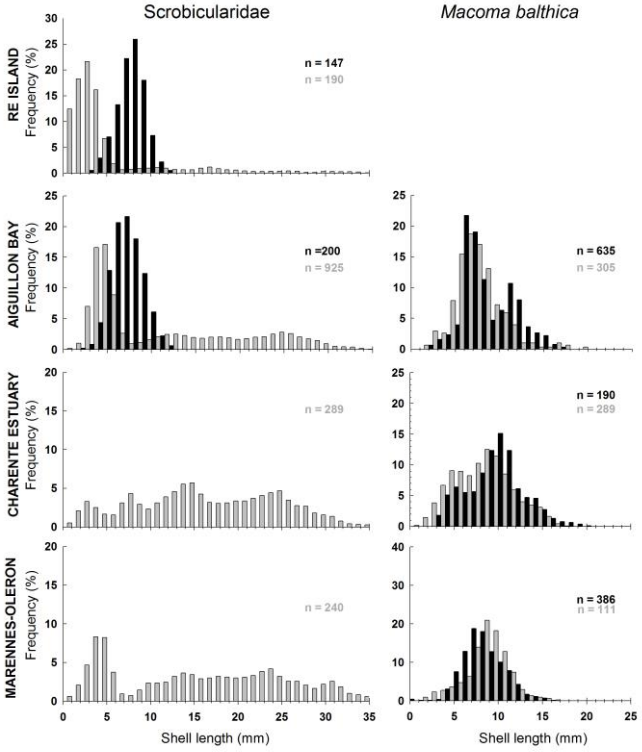

Figure 4.—Size-frequency distribution of main bivalve species consumed (mm), reconstructed from fragments found in droppings (black bars), compared to their size-frequency distribution in samples extracted from the sediment (grey bars).

PREY SELECTION

The distributions of the size classes of *M. balthica* consumed by godwits were similar to the distributions of size classes available at the sites with bare mudflats (Fig. 4). At AI_C, godwits extracted *M. balthica* with a mean length of 8.9 ± 2.9 mm (*n* = 635; mean ± SD) vs. 8.4 ± 2.1 (n = 172) found in the sediment (Kolmogorov-Smirnov test: D = 0.136, p = 0.98), at CE 10.0 ± 3.2 mm (*n* = 180) vs. 9.5 ± 2.9 (n = 191) (D = 0.153, p = 0.91) and at MO_M 9.6 ± 2.2 mm (n = 386) vs. 9.7 ± 2.1 (n = 79; D = 0.142, p = 0.98). Smaller individuals of Scrobiculariidae, either *A. tenuis* or *S. plana*, were consumed compared to those of *M. balthica*. Godwits selected individuals with a mean length of 7.6 ± 1.5 mm (n = 200) at AI_C, 8.7 ± 1.9 mm (n = 7) at RI_{FA} and 7.9 ± 1.2 mm (n = 140) at RI_{FL}. Godwits actively selected and preyed on the overlap in size classes between the largest *A. tenuis* and the smallest *S. plana* (Fig. 4).

FROM TOTAL RESOURCE TO AVAILABLE FOOD

The contribution of molluscs and seagrass species to the available food stock for godwits (Fig. 3b) was compared to the contribution of those same species to the total stock (Fig. 3a). The

species *H. ulvae*, *C. edule* and *Ruditapes* spp. (classified as "Others" in Fig. 3), together with the Scrobiculariidae, represented the majority of energy content for the total stock at all sites. On the three seagrass sites (Fig. 5), the plant represented at least 97 % of the energy content of the resources available.

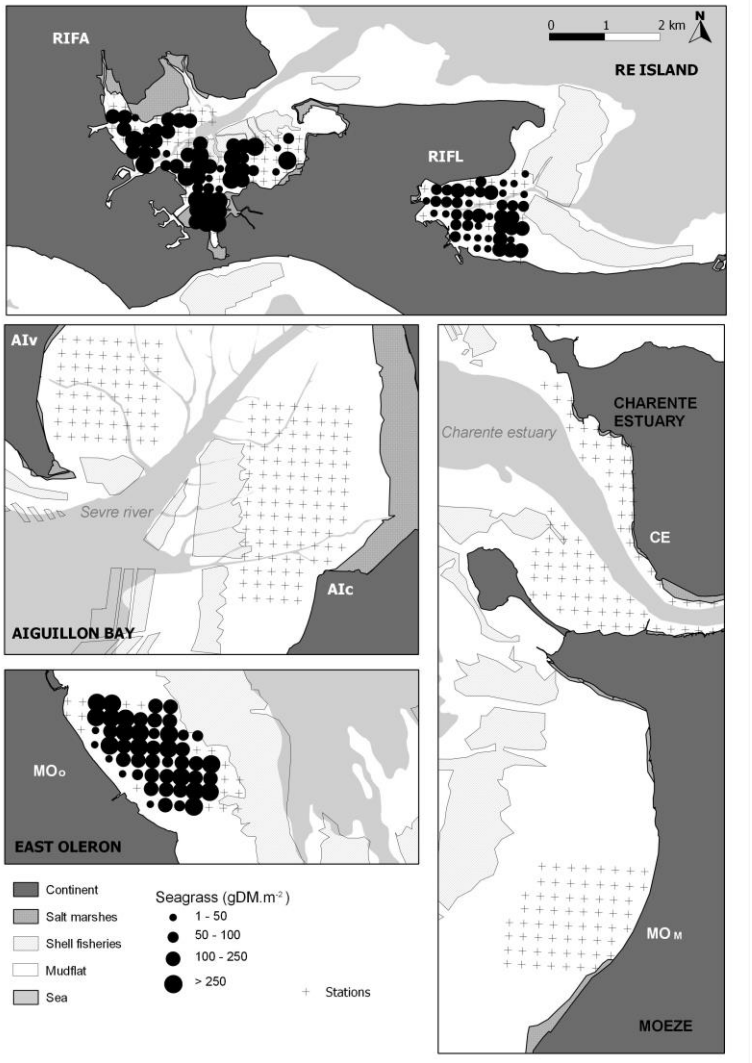

Figure 5.— Distribution of seagrass Z*ostera noltii* biomass in the Pertuis Charentais (leaves and rhizomes are considered together and expressed in $g_{DM}.m^{-2}$).

On bare mudflat sites, the Scrobiculariidae and *M. balthica* represented most of the available resources, accounting for at least 85 % of the energy content. Bivalves were widely distributed at all sites (frequency of occurrence between 82 and 100 %, Fig. 6). Nevertheless, the distribution of available bivalve resources at each site was not homogenous (Fig. 6). When we extracted the harvestable bivalve biomass from the total bivalve biomass per station, 59 % of the stations in RI_{FA} contained suitable food (excluding non-profitable or non-ingestible prey) and could be considered as potential feeding areas. The same is true for several stations in other sectors: 91 % in

RI_{FL}, 83 % in MO_O and 69 % in AI_V. *Macoma balthica* never exceeded 10 % of the total bivalve biomass per site but represented between 24 and 51 % of the harvestable bivalve biomass at any given location (Fig. 3).

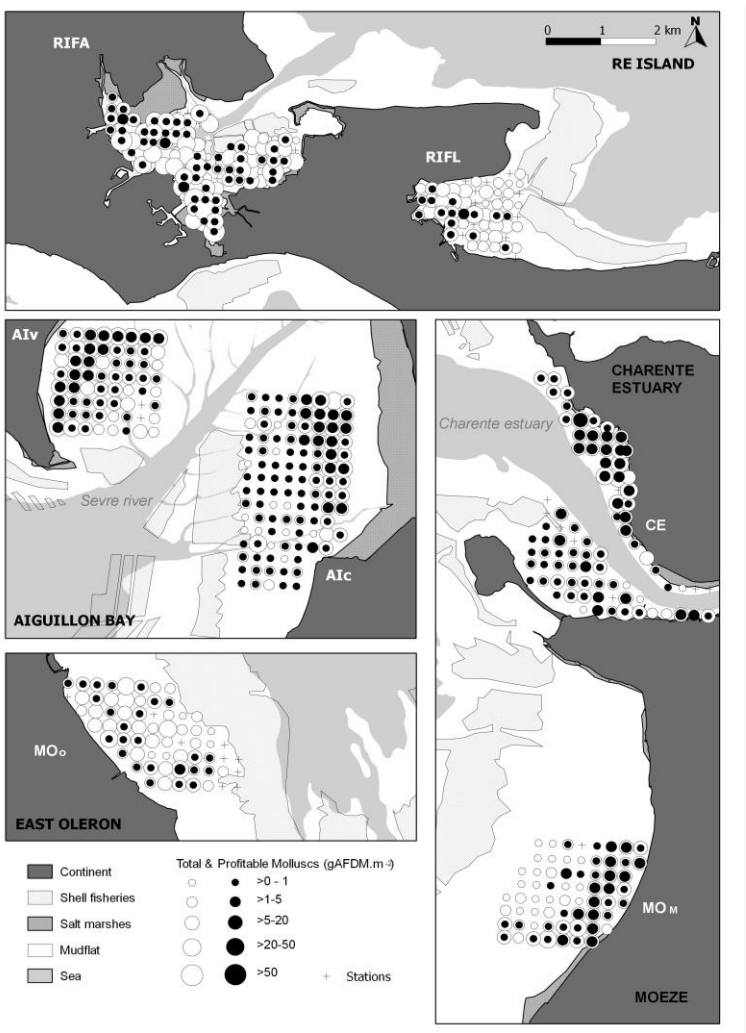

Figure 6.— Distribution of total (all mollusc species, open dots) and profitable (prey intake in 4–16 mm range, dark dots) biomasses of molluscs in the Pertuis Charentais ($g_{AFDM}.m^{-2}$).

The location of patches of available food differed between sites. In MO_M, the patches of food were located at higher levels of the mudflat, close to the coastline (Fig. 6). Although sampling was not carried out at the same time in CE and AI_C, the available bivalves were similarly distributed on the intertidal mudflats at these two sites.

PREY QUALITY

For all consumed prey sizes (4–15 mm size class ranges pooled), the mean digestive quality index of *M. balthica* (1.5 ± 0.6, n = 497) was significantly higher than that of *S. plana* (1.3 ± 0.6, n = 395) and also higher than that of *C. edule* (0.6 ± 0.3, n = 339; Kruskal-Wallis: χ^2 = 574.25, df =

3, $p < 0.001$). A multiple comparison test showed that *A. tenuis* has a similar digestive quality (1.7 ± 0.7, n = 51) to *M. balthica* for all sizes below 7 mm (Fig. 7).

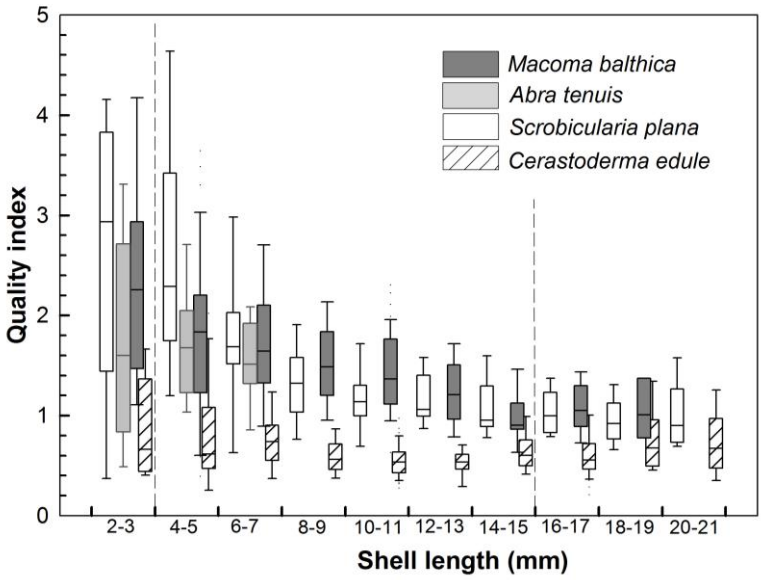

Figure 7.— Comparison of quality in the 2 mm class size of the main godwit prey at all study sites. Ingested prey ranges are delimited by the two vertical dashed lines.

DISCUSSION

The Icelandic Black-tailed Godwit is able to forage on a wide variety of habitats during its annual cycle, feeding on rice fields in Spain (Masero *et al.*, 2010), meadows in the Netherlands (Gerritsen & Tijsen, 2003) and marsh and dwarf-birch bogs in Iceland (Gunnarsson *et al.*, 2006). Nevertheless, most of the individuals wintering in Western Europe are restricted to intertidal mudflats (Gill *et al.*, 2007). On the central Atlantic coast of France, wintering Black-tailed Godwits use four sites at which they are restricted to only two types of habitat: bare mudflats and seagrass beds. They forage on seagrass habitat on Ré Island (Robin *et al.*, 2013) at which they adopt mainly a rhizovory diet. On bare mudflats, on the three others sites, they are strict carnivores and select predominantly the bivalve *M. balthica* followed by medium-sized Scrobiculariдae (large *A. tenuis* and/or small *S. plana*). Thus, they have clearly expanded into a herbivorous niche at a newly established wintering site, although the species was previously known as a carnivore (Robin *et al.*, 2013). Within sites, godwits target the most profitable preys. With the exception of disturbances, the distribution and movement of individuals within the Pertuis is largely influenced by the distribution, abundance and accessibility of only two prey organisms: the seagrass *Z. noltii* and the bivalve *M. balthica* and not by surface of favourable habitat like bare mudflat and seagrass bed.

The very high density of godwits in seagrass habitats (up to 4.1 individuals per hectare) compared to bare mudflat habitats (up to 1.4 individuals per hectare) and the low interference observed between congeners in flocks (dense flocks of around 800 individuals in the same feeding patch) indicate that this resource is likely to be sufficient to satisfy daily energy requirements.

Indeed, seagrass beds consist of widely available resources in which rhizomes, at high densities, seem to be indefinitely harvestable by godwits during the wintering period. The search efficiency of the patches is clearly reduced as godwits use the same feeding patch for a long time with limited movement (pers. obs.). If the searching of food patches is limited for seagrass habitats, the digestive process time could be much longer than when they feed on bivalves.

Therefore, we can wonder why the huge seagrass bed of Oléron Island was very poorly used with a maximum of only 100 individuals observed feeding (pers. obs.). We hypothesize that the coarser sediment grain on Oléron could limit the grazing capacity of godwits (Le Drean Quenec'Hdu *et al*., 1995). During grazing, godwits have to hammer their long bill quickly and deeply into the sediment in order to scrape the rhizomes of *Z. noltii* (pers. obs.). However, the sediment on the east coast of Oléron does not offer easy access to seagrass rhizomes, and it is unlikely to be compensated for by sufficient densities of available bivalves explaining the nearly absence of the species on site.

For individuals with a purely carnivorous diet, the selection of sites and, within these, of food patches, can be attributed to the density of available highest quality prey: *M. balthica*. This bivalve has been described as the best quality prey for molluscivorous shorebirds such as the Red Knot (*C. canutus*) at several wintering sites in Western Europe (Quaintenne *et al.*, 2010; Zwarts & Blomert, 1992). However, the handling time and research efficiency for each prey category should also be considered (Leeman *et al*., 2001; Piersma *et al*., 1995; van Gils *et al*., 2004). On the studied bare mudflats, the majority of the macrofaunal biomass is made up of the bivalves *C. edule*, the large and medium-sized *S. plana*, and the mudsnail *H. ulvae*. Nevertheless, these preys were never or rarely taken by godwits. *C. edule* because of its lowest dietary value for godwits (Fig. 7), and most of the *S. plana* were too large to be ingested. The mudsnail is preyed upon predominantly by the Red Knot *C. canutus* and Common Shelduck *Tadorna tadorna* wintering in the area (Quaintenne *et al.*, 2010; Viain, 2008). This very abundant food resource occurs at every site with high accessible densities (< 4 cm in depth), resulting in high predictability for the birds. The seagrass habitats have the highest densities of *H. ulvae* in the area but godwits ignore this prey due to its costly handling time.

A largest proportion of the local wintering population of godwits used Aiguillon Bay. This traditional site welcomes a stable wintering population and individuals stay one month later in Aiguillon Bay than at the other three sites. Indeed, in January, food remained widely distributed across the whole mudflat compared to the southern sites (Fig. 6, Tab. I) and the longer stay of godwits in Aiguillon Bay (until March) could be due to the higher quality of this site with high density and large distribution of the highest quality prey: *M. balthica*. At southern sites, the number of individuals was less stable. The individuals roosting on the high tide roost at Moëze were linked to individuals roosting in the nature reserve of Yves marshlands (Fig. 1). This North to South movement of godwits was previously described by Robin *et al.* (2013) and could be due to food depletion in Yves Bay. The Charente Estuary is located exactly midway between both high tide roosts (around 9 km apart) and the available biomass of *M. balthica* is high in the autumn.

Just as predicted by the previously demonstrated 'buffer effect' (Gill *et al*., 2001), with increasing population size in France (Triplet *et al.*, 2007), new sites filled up and at one of those the godwits started to feed on rhizomes in a seagrass-bed without *Macoma* (Robin *et al.*, 2013). Nevertheless, there may be other reasons than prey quality to explain the choice for Ré Island, which is settled even before Yves/Marennes-Oléron where birds eat bivalves again. In winter, coastal wetlands in France tend to be disturbed by hunters. When the totally protected area in Aiguillon Bay became filled up, godwits were left with a choice between the coastline of Yves/Marennes-Oléron partly disturbed by hunters and the undisturbed area at Ile de Ré (Robin *et al.*, 2013). Further studies appear as necessary to show whether a comparison of the energy balance of Black-tailed Godwits at the four sites demonstrates any difference (cf. Quaintenne *et al*., 2011).

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